Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest

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Abstract: Aims Litterfall, as an important link between aboveground and belowground processes, plays a key role in forest ecosystems. Here, we test for effects of tree species richness on litter production and litter quality in subtropical forest. The study further encompasses a factorial gradient of secondary succession that resulted from human exploitation. Given that a large percentage of subtropical forests are in secondary successional stages, understanding the role of biodiversity on forest re-growth after disturbance appears critical. Methods From January 2009 to December 2014, we monitored forest litterfall in 27 Comparative Study Plots that spanned a gradient of tree species richness (3–20 species) and secondary successional ages (20 to 120 years) in Gutianshan Natural Nature Reserve, Zhejiang Province, China. The experiment is part of the biodiversity–ecosystem functioning research platform 'BEF-China'. Tree litterfall was collected in monthly intervals using litter traps. Samples were separated into leaf and non-leaf components. Leaf litter was further sorted into dominant and other species. Community level monthly leaf litter C and N contents were analysed through a full year. General linear mixed-effects models were applied to test for effects of tree species richness and successional age on litter quantity and leaf litter C/N. Important Findings Litterfall increased with species richness among and within successional age and this effect was consistent across years. Successionally older stands had higher litterfall and this effect was related to increased tree species richness. However, species richness did not change the intra- and inter-annual temporal stability of litterfall. Increasing tree species richness increased leaf litter quality (decreased C/N), while successional age had no effect. Our study indicates that more diverse forest stands produce more leaf litter and that this litter has higher N concentrations, which could promote forest growth through accelerated nutrient re-cycling.

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Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest

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Abstract

Aims

Litterfall, as an important link between aboveground and belowground processes, plays a key role in forest ecosystems. Here, we test for effects of tree species richness on litter production and litter quality in subtropical forest. The study further encompasses a factorial gradient of secondary succession that resulted from human exploitation. Given that a large percentage of subtropical forests are in secondary successional stages, understanding the role of biodiversity on forest re-growth after disturbance appears critical.

Methods

From January 2009 to December 2014, we monitored forest litterfall in 27 Comparative Study Plots (CSPs) that spanned a gradient of tree species richness (3 – 20 species) and secondary successional ages (~ 20 – 120 years) in Gutianshan Natural Nature Reserve, Zhejiang Province, China. The experiment is part of the biodiversity–ecosystem functioning research platform “BEF-China”. Tree litterfall was collected in monthly intervals using litter traps. Samples were separated into leaf and non-leaf components. Leaf litter was further sorted into dominant and other species. Community level monthly leaf litter C and N contents were analysed through a full year. General linear mixed-effects models were applied to test for effects of tree species richness and successional age on litter quantity and leaf litter C/N.

Important Findings

Litterfall increased with species richness among and within successional age and this effect was consistent across years. Successionally older stands had higher litterfall, and this effect was related to increased tree species richness. However, species richness did not change the intra and inter-annual temporal stability of litterfall. Increasing tree species richness increased leaf litter quality (decreased C/N), while successional age had no effect.

Our study indicates that more diverse forest stands produce more leaf litter and that this litter has higher N concentrations, which could promote forest growth through accelerated nutrient recycling.

Keywords: species richness, BEF-China, litterfall, leaf litter C/N, subtropical forest, secondary succession, structural equation models

Introduction

Above- and belowground carbon dynamics are linked through litterfall, which thus is a key determinant of forest ecosystem functioning (Sayer *et al*., 2010). Positive effects of tree species richness on forest productivity have been found in several recent studies (Barrufol *et al.*, 2013, Morin *et al.*, 2011, Zhang *et al.,* 2012, Chen *et al.,* 2016, Chisholm *et al*., 2013, LaManna *et al*., 2016). However, diversity effects on litter production and litter quality have received less attention.

Previous studies have found a positive correlation between net primary productivity (NPP) and litterfall, with aboveground litter fluxes accounting for approximately one third of NPP (Clark *et al*., 2001a, Gower *et al*., 1997, He *et al*., 2012, Nouvellon *et al*., 2012). Increased productivity in more diverse forest (Baruffol *et al.*, 2013) raises the possibility that litter production increases with species richness, which might lead to faster nutrient cycling. However, nutrient losses and re-cycling rates also depend on leaf litter quality (Li *et al.*, in press). One of the important indicators of leaf litter quality is its carbon to nitrogen ratio (C/N), which depends on leaf nutrient status and nutrient resorption and reflects the nutrient-use strategies of species and individuals (Vitousek, 1984). At the community level, the quality of forest leaf litter will likely depend on the species composition of tree stands. Apart from that, leaf litter quality of the same species may also change with the diversity of the community in which they grow.

Positive effects of tree species richness on litterfall have been found in a tropical forest biodiversity experiment (Scherer-Lorenzen *et al.,* 2007), but only at low diversity levels (3-species mixtures compared with monocultures), with no additional effect of a higher species richness level (6-species mixtures). In the same study, effects on leaf litter C and N content were highly species-specific (Scherer-Lorenzen *et al.,* 2007). A number of studies have compared litterfall in monocultures to litterfall in natural forests (e.g. Yang *et al*., 2004). However, natural forests generally have a more complex stand structure and differ in demographic dynamics, so that it is difficult to infer effects of tree species richness from a comparison with planted monocultures (Coursolle *et al*., 2012, He *et al.,* 2012, Yang *et al.,* 2011).

With the rapid increase in the human exploitation of natural resources, an increasing number of forests are in secondary successional stages. At later successional stages, tree growth slows down compared to younger stands (Chi *et al*., in press). Older stands generally are characterized by a higher number of canopy species, fewer shade-tolerant species, higher standing biomass (Baruffol *et al*., 2013) and a higher investment into defense against herbivores and pathogens leading to lower leaf N content (Bruelheide *et al.,* 2011, Kröber *et al.,* 2012). For these reasons, effects of tree species richness on litterfall may depend on stand age.

To date, long-term investigations of the relationship between biodiversity and litterfall quantity and quality in natural forests with complex structure are scarce. It thus remains unclear how species richness contributes to the restoration of ecosystem processes and services through secondary forest succession.

Here, we measured tree litter production for six years in plots spanning largely independent gradients of tree species richness and forest successional age in species-rich subtropical forest. We hypothesized that (1) litterfall increases with species richness and that this effect increases with successional age; (2) tree species richness decreases leaf litter C/N, i.e. improves leaf litter quality, and more strongly so in later successional stages.

Materials and Methods

Study site

The present study was carried out in Gutianshan National Nature Reserve in the western part of Zhejiang Province, China (29° 8' 18" – 29° 17' 29" N, 118° 2' 14" – 118° 11' 12" E). This region has a typical subtropical monsoon climate with an annual average temperature of 15 °C and annual average precipitation of *ca.* 2000 mm. The bedrock is comprised of granite and gneiss. Sandy-loamy and silty-loamy acidic Cambisols with pH ranging from 4 to 5 are the predominant soil type (Geißler *et al.*, 2010).

Deforestation at the study site occurred during different periods since the 1950s, resulting in a patch structure with respect to successional age. Forest patches also vary in species richness, presumably due to variation in seed rain, natural recruitment and environmental conditions. In 2009, we established 27 plots with a size of 30 x 30 m each, called Comparative Study Plots (CSPs). These plots span factorial gradients in tree diversity and successional ages (Bruelheide *et al.*, 2011, Table S1 (Supplementary Data)). Stand age was defined as the age of the fifth-largest tree in a plot, with age determined from a stem core (Bruelheide *et al.*, 2011). Because age is not a precise metric, we assigned plots to three age classes (young forest: 20 – 50; medium forest: 50 – 80; old forest: > 80 years old).

In 2008, an inventory was conducted to assess tree species composition of each plot (Baruffol *et al.*, 2013). Canopy trees, defined here by a diameter at breast height of at least 10 cm, comprised 1523 individuals belonging to 66 species, 49 genera, and 29 families. In the present study, we use canopy tree species richness as metric of biodiversity for all analysis. The reason for this choice was that the litter traps we used were installed 1.5 m above ground and therefore mainly collected litter from canopy trees. Similar to successional age, plot-level tree species richness was categorized into three classes (low: 3 – 8, medium: 9 – 13, high: 14 – 20 species) to reflect the deliberate selection of plots belonging to these three richness categories.

Litterfall

In December 2008, four litter traps were set up in the corners of the central 10 × 10 m quadrat plus one in the middle of each plot. A nylon net (1 mm mesh) with a horizontal trapping area of 0.75 × 0.75 m was placed over a PVC frame 1.5 m above the ground.

Litterfall was collected monthly from January 2009 to December 2014. In December 2010 and July 2011, litter could not be collected because of heavy snow and rainstorm. Litterfall of these months was collected together with litter from the next month, and this amount was partitioned among the respective months based on the litter distribution in the other years. In 2010 and 2011, litter was first separated into leaf and non-leaf litter. The leaf litter was then sorted into the dominant species (*Castanopsis eyrei*, *Schima superba*, *Pinus massoniana*, *Cyclobalanopsis glauca*, *Quercus serrata* var. *brevipetiolata*, *Lithocarpus glaber*) and other evergreen and deciduous litter. The number of other evergreen and deciduous litter species per trap was also recorded from January to March of year 2010 and from April to December of year 2011. Non-leaf litter included fine branches (≤ 2.5 cm in diameter), bark, reproductive structures, animal detritus and other unidentified fine litter.

Litter was weighed after oven-drying at 80°C for 24 h. Leaf litter samples of the year 2010 were pooled by plot, ground using a ball mill (NM200, Retsch, Haan, Germany), and C and N concentrations determined by dry combustion (2400 II CHN elemental analyzer, Perkin-Elmer, USA).

Statistical analyses

The effects of year (1 – 6), month (1 – 12), successional age (1 – 3), species richness (3 – 20) and their interactions on the litterfall and leaf litter quality were analyzed with linear mixed-effects models using ASReml-R (Butler *et al.*, 2007). All fixed-effects terms in the model were fitted sequentially. Litterfall amounts were square root-transformed prior to analysis to meet the requirements of normal distribution and homoscedasticity of residuals.

For yearly litterfall data, the fixed-effects terms were fitted in this sequence: YEAR + div + lin(age) + AGE + YEAR × div + YEAR × lin(age) + YEAR × AGE + div × lin(age) + div × AGE. The random-effects terms used were plot, modeling the random sampling of plots, and the interaction plot×YEAR, which corresponded to the residual. Interactions are denoted by a × operator. Capitalized terms YEAR (6 levels) and AGE (3 levels) are factors, while lin(age) is a continuous integer variable, i.e. the linear contrasts of factor AGE. Similarly, div is a continuous integer variable and stands for species richness.

Monthly litterfall data were analyzed with a mixed-effects model with plot, plot × MONTH and plot × YEAR as random effects and factor MONTH (12 levels), species richness, successional age and their interactions as fixed terms. Leaf C/N was analyzed similarly excluding terms containing YEAR.

Because plot species richness was positively correlated with successional age ($r = 0.64$, $P < 0.01$), we reversed the order of tree species richness and successional age to investigate the degree of confounding between their effects (Baruffol *et al.*, 2013; Schmid *et al.*, in press). Species richness effects fitted before successional age indicated the overall species richness effect, whereas richness fitted after successional age indicated effects of species richness after adjusting for successional age (i.e. effects of species richness within successional age).

Results

Environmental effects

Site conditions (Table S1), including elevation, slope, aspect, slope inclination, soil pH, soil moisture and soil total C and N content did not correlate significantly with tree litterfall or leaf litter C/N (Pearson's product moment correlations, $P > 0.05$).

Litterfall quantity

Annual litterfall varied among years and plots, ranging from 2.6 Mg ha^{-1} yr^{-1} to 7.9 Mg ha^{-1} yr^{-1}, with a mean value of 5.4 Mg ha^{-1} yr^{-1}.

Canopy tree species richness significantly positively affected yearly total litterfall (Fig. 2a, Table 1a, $P < 0.001$ in mixed-effects model when div was fitted before lin(age) and AGE; $P < 0.05$ when div was fitted after lin(age) and AGE). The positive effect of species richness was also observed in a structural equation model (Fig. S1 (Supplementary Data)). The positive effect of species richness was similar at different successional ages (Fig. 2a, Table 1a, $P = 0.64$ for div × lin(age)). Species richness effects were independent of year (Table 1a, $P > 0.05$ for YEAR × div).

Yearly litterfall increased with forest stand age if influences of species richness were ignored (Fig. 2a, Table 1a, $P < 0.01$ for lin(age) fitted before div). However, the main effect of successional age became statistically insignificant when it was adjusted for species richness (Table 1a, $P > 0.1$ for lin(age) fitted after div). The notion that age effects might have been mediated by species richness changes was supported by structural equation modelling (Fig. S1, no significant direct path from successional age to litterfall). Litterfall gradually increased with year (Fig. 1, anova with lin(year) as continuous variable, $F_{1,134} = 18.27$, $P < 0.01$), and this effect was more pronounced in medium or old forest (Fig. 1).

The analysis of monthly litterfall data revealed a dependence of species richness effects on season (Table 1b, $P < 0.01$ for MONTH × div; Fig. 3). Different litterfall components had different monthly dynamics (Fig. 3). Leaf litterfall showed a bimodal temporal trend, whereas non-leaf litterfall did not. Positive species richness effects were found for total and leaf litterfall only in months with high litter production (Apr. – May, Oct. – Nov.; Fig. 3a, b).

Neither the intra-annual (seasonal) nor the inter-annual stability of litterfall production depended on species richness (Fig. 3, Fig. S2 (Supplementary Data)).

Litter species composition

Higher species numbers were found in the traps in more species-rich plots, especially in months with high litterfall (Fig. 5). As for litterfall, litter species richness followed a bimodal temporal pattern for evergreen species, but a unimodal pattern for deciduous species (Fig. 5). In general, litterfall from the highly productive dominant species *Schima superba* and *Castanopsis eyrei*, as well as other evergreen and other deciduous species, was higher in species-rich plots and in later successional stages (Fig. 6).

Leaf litter C/N

Leaf litter C/N, a proxy for litter quality, averaged 46.4 ± 1.1 g C $(g\ N)^{-1}$ (50.2% ± 14% C; 1.1% ± 3% N). Total leaf litter C return was 1720 ± 123 kg C ha^{-1} yr^{-1} and N return 38.6 ± 2.8 kg N ha^{-1} yr^{-1}. Leaf litter C/N decreased significantly with increasing tree species richness (Fig. 2b, Table 1c, $P < 0.05$ with div fitted before lin(age) and

AGE; *P* < 0.05 with div fitted after lin(age) and AGE). Leaf C/N did not depend on successional age (Fig. 2b, Table 1c, *P* > 0.05 for lin(age) and AGE fitted before or after log(div)).

Discussion

Our results showed a strong positive effect of species richness on both litterfall amounts and litter quality (Tables 1a, b). This finding parallels strong positive, density-mediated tree diversity effects on stand total basal area and growth in the same plots (Baruffol *et al*. 2013). Baruffol *et al*. (2013) argued that the larger number of tree individuals found in more diverse plots possibly resulted from complementarity among species, i.e. that more complementarity among species reduced competition among heterospecific trees and allowed for denser stands at higher species richness. Belowground benefits from complementarity may also have contributed to higher total leaf production (Bessler *et al.*, 2009; Bu *et al.,* in press; Sun *et al.,* in press). Interestingly, positive effects of species richness on leaf area were also found in a designed experiment with constant tree density (Peng *et al.,* in press). The increase in litterfall with diversity may thus also be caused by higher leaf production of individual trees in more diverse forest stands (Clark *et al*., 2001a). Overall, this suggests that more diverse forest stands produce more leaf litter, and that this effect can but must not necessarily be mediated by an increased density of tree individuals, but also by increasing leaf production.

The higher leaf litter nitrogen contents in more diverse plots may indicate an improved supply of trees with nitrogen and/or a lower nutrient resorption efficiency. In forests, nutrient concentrations of newly fallen leaf litter often correlate positively with nutrient concentrations of fresh leaves (Aponte *et al.*, 2013). An additional possible explanation for the observed effects in our study is that the fraction of deciduous broadleaf trees increased with species richness (Fig. 6a). These species generally have higher green fresh leaf N concentrations than evergreen or conifer species (Han *et al.*, 2005, Kröber *et al.*, 2012, McGroddy *et al.*, 2004). It is concievable that this change in species composition with increasing species richness was part of the mechanism underlying the positive species richness effects on litterfall N fluxes. Because the quality of litterfall is a major controller of litter decomposition and nutrient return rates (Manzoni *et al*., 2008, Meier *et al*., 2008), the lower initial litter C/N ratio in more species-rich plots in our study could accelerate decomposition and nitrogen mineralization. Tree species diversity might thus promote productivity by increasing nutrient availability.

The species richness effects we found were independent of successional age. Our hypotheses, predicting a stronger biodiversity effect in later successional stages were rejected. This suggests that even in young forests tree species diversity already plays an important role. Higher litterfall in old successional forests has been attributed to higher standing leaf canopy as well as decreased physiological function of older trees (Drake *et al.*, 2011). Our analysis suggests that increased species richness may be a further factor affecting increased litter fall in older secondary forests, which is consistent with the effects on woody growth pattern (Baruffol *et al.*, 2013; Fig. S1, Tables 1a, b).

Our findings contrast with those of other studies in which no significant effects of tree diversity on litter production and litter N content were found (Scherer-Lorenzen *et al.*, 2007). However, in those previous studies lower diversity levels were compared (species richness levels 1, 3, 6) whereas in our study the range of species richness values was considerably higher (3 – 20 species).

In our study we did not find a significant effect of successional age on the leaf litter C/N (Table 1c). This does not support the assumption that there should be a change in resource-use strategy from high nutrient acquisition to nutrient retention along forest succession. It also does not support the assumption that trees should increasingly allocate more energy to defense which may decrease leaf litter quality (Kröber *et al.*, 2012). However, regarding the first assumption, nutrient resorption efficiency may also be higher in earlier successional stage, serving the higher demand for nutrients in faster-growing trees (Yuan *et al.*, 2010). Regarding the second assumption, former research in the same study plots has shown that while green leaf physical resistance increased, chemical defense traits, such as tannin and phenolics, decreased with forest successional age, such that the litter decomposition rates remained stable along secondary succession (Eichenberg *et al.*, 2014). Positive and negative effects may have acted together and thus caused the balanced leaf litter C/N across successional age in our study plots.

In conclusion, tree species diversity rather than forest successional age seemed to play the major role in affecting leaf litter quantity and quality. Higher litterfall production and better leaf litter quality in more diverse forest stands could promote higher soil microbial and fauna diversity and create more favorable conditions for decomposition and nutrient release, thus stimulating increased tree growth.

Supplementary Data

We present the following supplementary data:

Table S1: Topography and soil information for the 27 Comparative Study Plots.

Figure S1: Structural equation model.

Figure S2: Litterfall stability as function of species richness.

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Table 1: results of three alternative sequential mixed-effects models for yearly, monthly litter production and leaf litter C/N

(a) yearly litterfall data from 2009 – 2014

	model 1			model 2	
Fixed terms	*F*-value		Fixed terms	*F*-value	
YEAR	F(5,115)=26.51	***	**YEAR**	F(5,115)=26.51	***
div	F(1,21)=11.47	***	**lin(age)**	F(1,21)=9.82	**
lin(age)	F(1,21)=1.55	n.s.	AGE	F(1,21)=0.12	n.s.
AGE	F(1,21)=1.42	n.s.	**div**	F(1,21)=4.50	*
YEAR×div	F(5,115)=2.14	.	**YEAR×lin(age)**	F(5,115)=3.71	**
YEAR×lin(age)	F(5,115)=2.26	.	**YEAR×AGE**	F(5,115)=2.63	*
YEAR×AGE	F(5,115)=3.61	**	YEAR×div	F(5,115)=1.67	n.s.
div×lin(age)	F(1,21)=0.00	n.s.	lin(age)×div	F(1,21)=0.00	n.s.
div×AGE	F(1,21)=0.23	n.s.	AGE×div	F(1,21)=0.23	n.s
Random terms	Variance component		Standard error of variance component		
plot	3.0437		1.0179		
residuals	1.5172		0.2001		

(b) monthly litterfall data from 2009 – 2014

	model 1			model 2	
Fixed terms	*F*-value		Fixed terms	*F*-value	
MONTH	F(11,253)=81.68	***	**MONTH**	F(11,253)=81.68	***
div	F(1,21)=9.91	**	**lin(age)**	F(1,21)=7.73	*
lin(age)	F(1,21)=0.97	n.s.	AGE	F(1,21)=0.02	n.s.
AGE	F(1,21)=0.96	n.s.	**div**	F(1,21)=4.08	.
MONTH×div	F(11,253)=1.88	*	**MONTH×lin(age)**	F(11,253)=1.84	*
MONTH×lin(age)	F(11,253)=1.26	n.s.	MONTH×AGE	F(11,253)=0.51	n.s.
MONTH×AGE	F(11,254)=1.07	n.s.	**MONTH×div**	F(11,253)=1.86	*
lin(age)×div	F(1,21)=0.00	n.s.	lin(age)×div	F(1,21)=0.00	n.s.
AGE×div	F(1,21)=0.73	n.s.	AGE×div	F(1,21)=0.73	n.s.
Random terms	Variance component		Standard error of variance component		
plot	0.2071		0.0905		
plot × YEAR	0.2526		0.0359		
plot × MONTH	0.4306		0.0459		
residuals	2.5165		0.0372		

(c) monthly leaf litter C/N data of year 2010

	model 1			model 2	
Fixed terms	*F*-value		Fixed terms	*F*-value	
MONTH	F(11,249)=13.69	***	**MONTH**	F(11, 249)=13.59	***
log(div)	F(1,21)=6.86	*	lin(age)	F(1,21)=0.26	n.s.
lin(age)	F(1,21)=2.90	n.s.	AGE	F(1,21)=1.37	n.s.
AGE	F(1,21)=0.075	n.s.	**log(div)**	F(1,21)=7.72	*
MONTH×log(div)	F(11,248)=0.51	n.s.	MONTH×lin(age)	F(11, 248)=0.62	n.s.
MONTH×lin(age)	F(11,249)=0.88	n.s.	MONTH×AGE	F(11, 250)=0.81	n.s.
MONTH×AGE	F(11,250)=0.89	n.s.	MONTH×log(div)	F(11,249)=0.84	n.s.
log(div)×lin(age)	F(1,21)=0.78	n.s.	lin(age)×log(div)	F(1,21)=0.78	n.s.
Log(div) ×AGE	F(1,21)=0.06	n.s.	AGE×log(div)	F(1,21)=0.06	n.s.
Random terms	Variance component		Standard error of variance component		
plot	23.83		8.137		
plot × MONTH	21.44		2.707		
residuals	41.93		1.671		

F values and corresponding degrees of freedom (numerator and denominator d.f.) are given in brackets. YEAR (6 levels), AGE (3 levels) MONTH (12 levels) are fixed-effects factors, while div, log(div) and lin(age) are continuous integer variables, i.e. lin(age) the linear contrasts of the factor AGE. The fixed-effect term div stands for canopy tree species richness, log(div) for the logarithm of div. Fixed-effects terms in bold face indicate significance: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. Marginal significance: · $P < 0.1$, not significant: n.s.).

Figure legends

Figure 1: total litterfall per year in different successional ages (see legend inside figure). Thick solid line indicates the linear regression line based on the 27 plot means pooled across successional ages. The grey shadow shows the 95% confidence interval.

Figure 2: (a) total litterfall per year and (b) leaf litter C/N (mass ratio) as functions of species richness in different successional ages. Error bars indicate means ± standard errors (n = 6 for total litterfall, n = 12 for C/N).

Figure 3: (a) total monthly litter production, (b) monthly leaf litter production and (c) monthly non-leaf litter production at different species richness levels. Error bars indicate means ± standard errors (n = 9). Circles with solid line refer to high-diversity plots; squares with dashed line refer to medium-diversity plots; triangles with dotted line refer to low-diversity plots.

Figure 4: monthly leaf C/N (mass ratio) at different species richness levels. Error bars indicate means ± standard errors (n = 9). Circles with solid line refer to high-diversity plots; squares with dashed line refer to medium-diversity plots; triangles with dotted line refer to low-diversity plots.

Figure 5: monthly litter species number per trap at different species richness levels for deciduous and evergreen species and for all species combined. Error bars indicate means ± standard errors (n = 9). Circles refer to high-, squares to medium- and triangles to low-diversity plots.

Figure 6: production of different species' leaf litter at (a) different species richness levels and (b) along different successional stages (see legends inside figure). Error bars indicate means ± standard errors (n = 9).

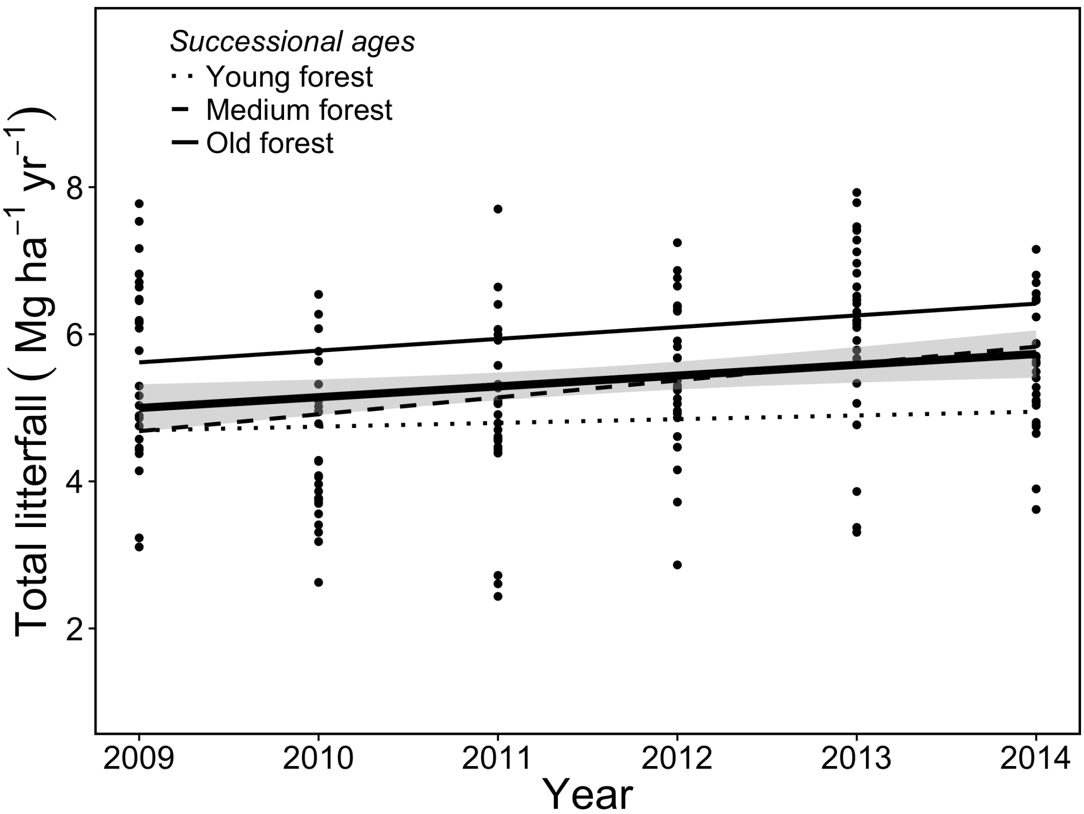

Figure 1: total litterfall per year in different successional ages (see legend inside figure). Thick solid line indicates the linear regression line based on the grand mean (n=27). The grey shadow shows the 95% confidence interval.

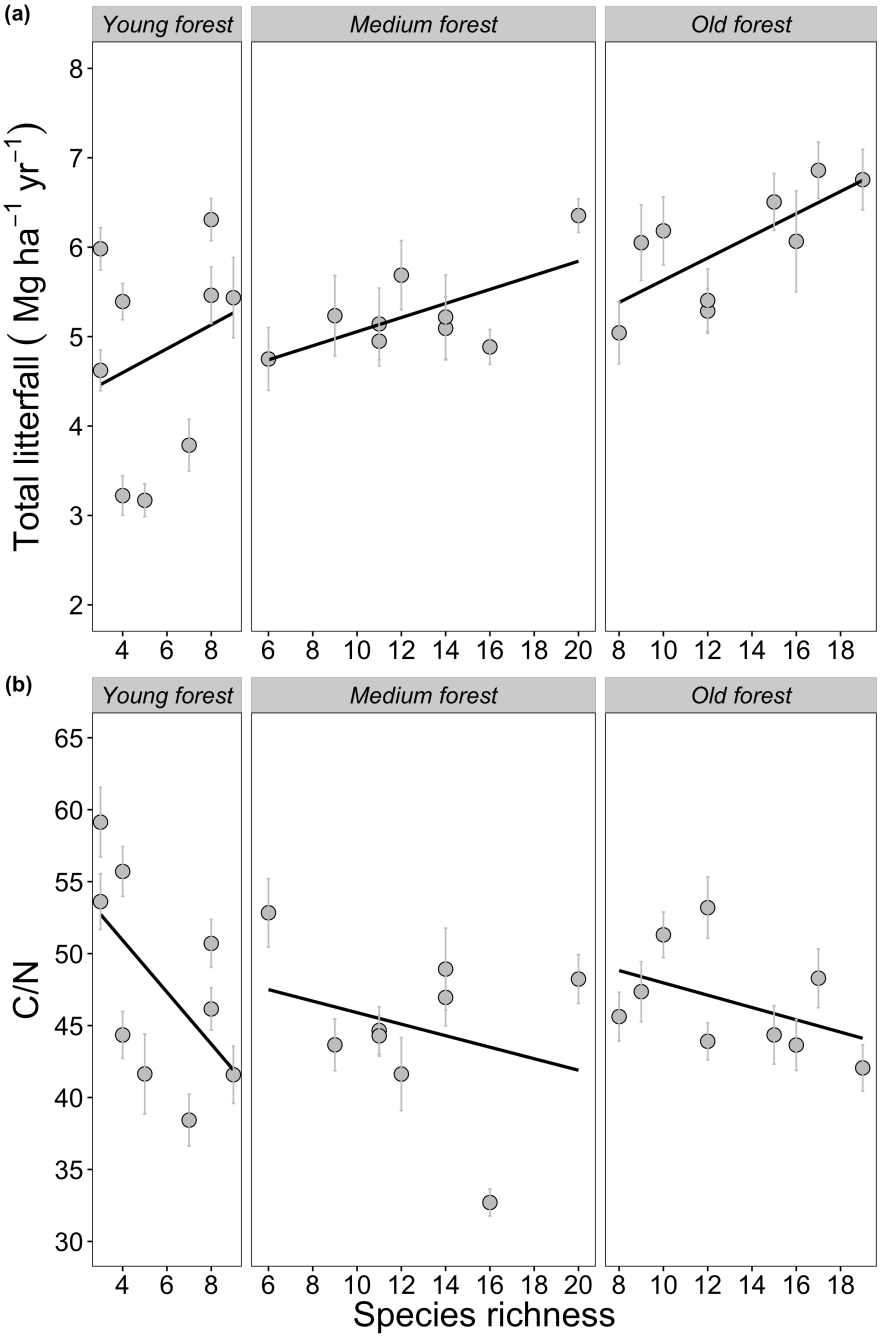

Figure 2: (a) total litterfall per year and (b) leaf litter C/N (mass ratio) as functions of species richness in different successional ages. Error bars indicate means ± standard errors (n = 6 for total litterfall, n = 12 for C/N).

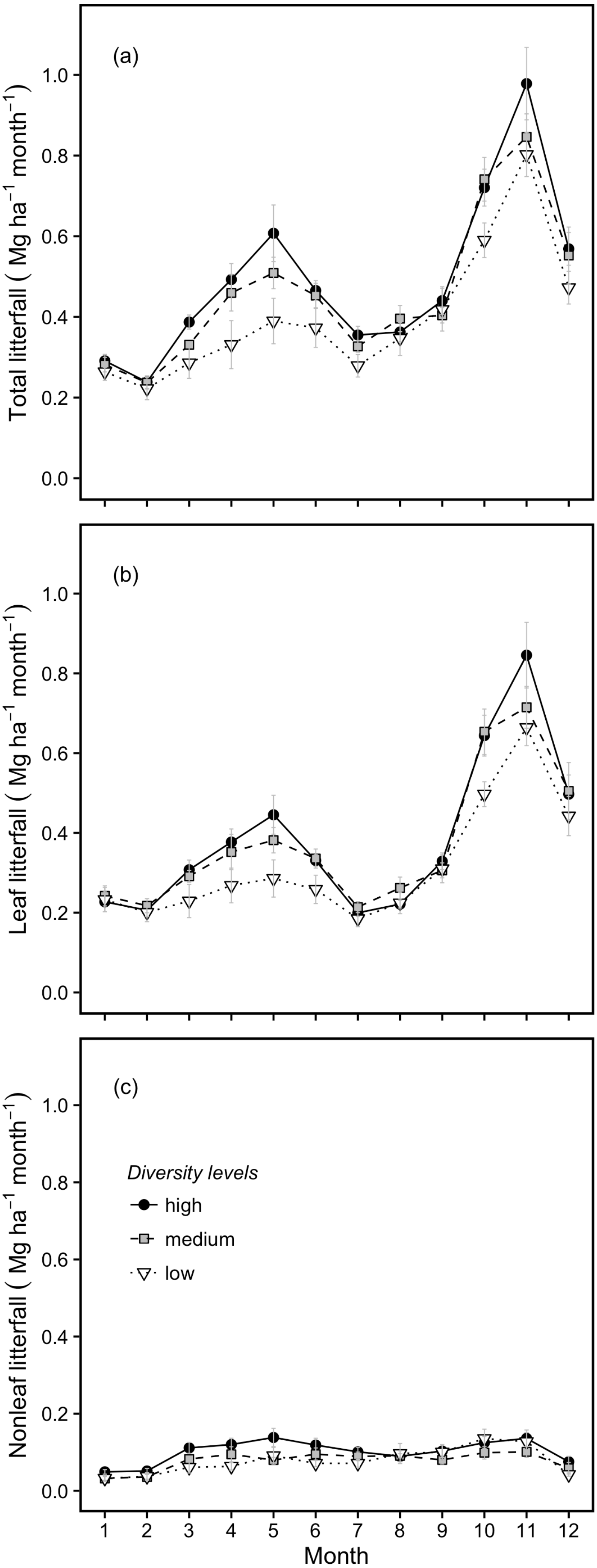

Figure 3: (a) total monthly litter production, (b) monthly leaf litter production and (c) monthly non-leaf litter production at different species richness levels. Error bars indicate means ± standard errors (n = 9). Circles with solid line refer to high-diversity plots; squares with dashed line refer to medium-diversity plots; triangles with dotted line refer to low-diversity plots.

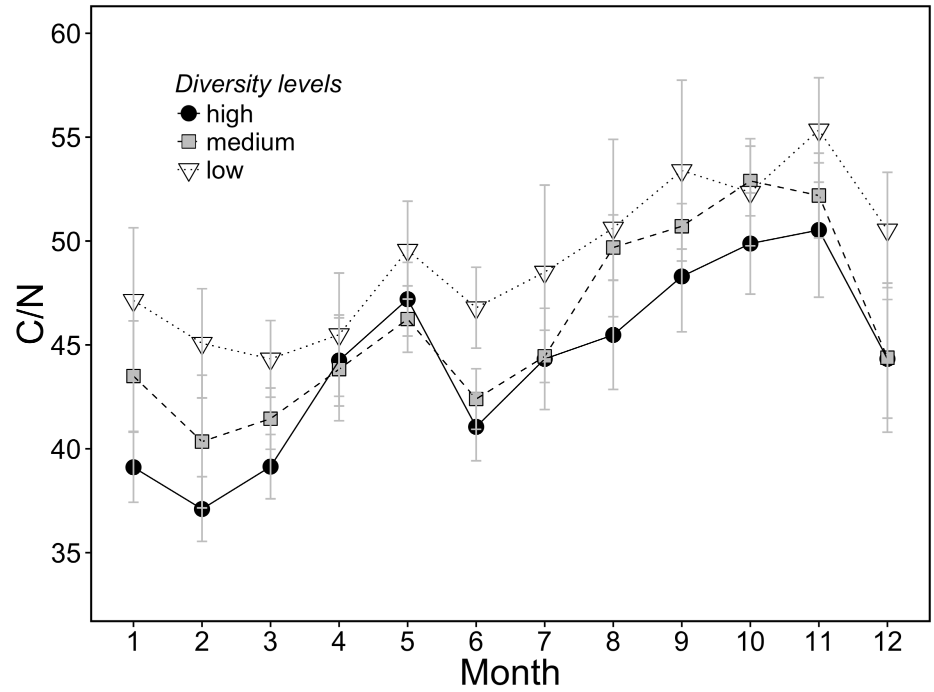

Figure 4: monthly leaf C/N (mass ratio) at different species richness levels. Error bars indicate means ± standard errors (n = 9). Circles with solid line refer to high-diversity plots; squares with dashed line refer to medium-diversity plots; triangles with dotted line refer to low-diversity plots.

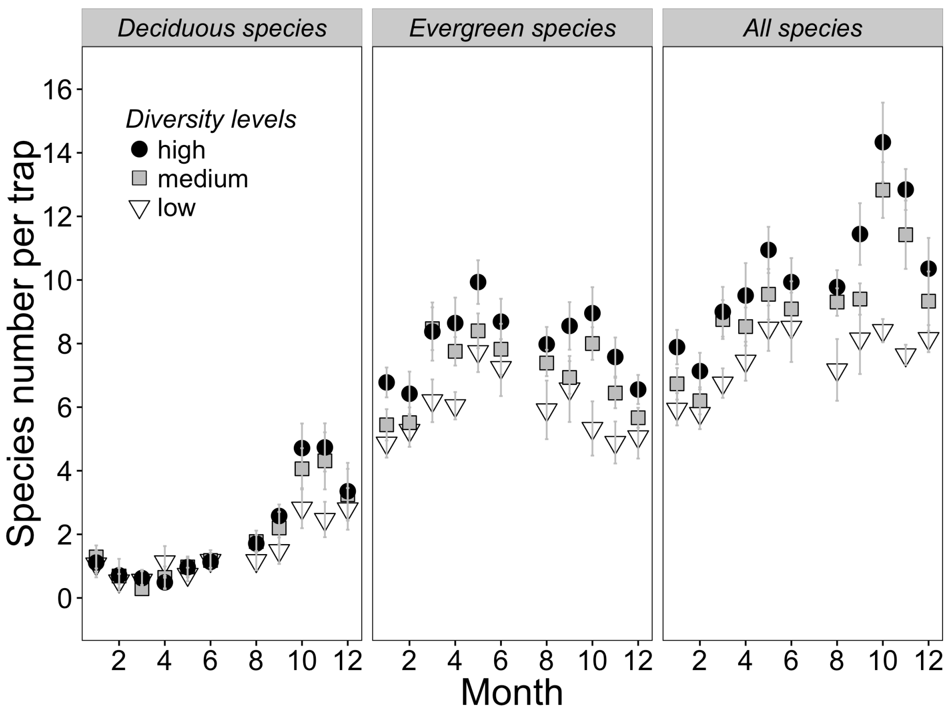

Figure 5: monthly litter species number per trap at different species richness levels for deciduous and evergreen species and for all species combined. Error bars indicate means ± standard errors ($n = 9$). Circles refer to high-, squares to medium- and triangles to low-diversity plots.

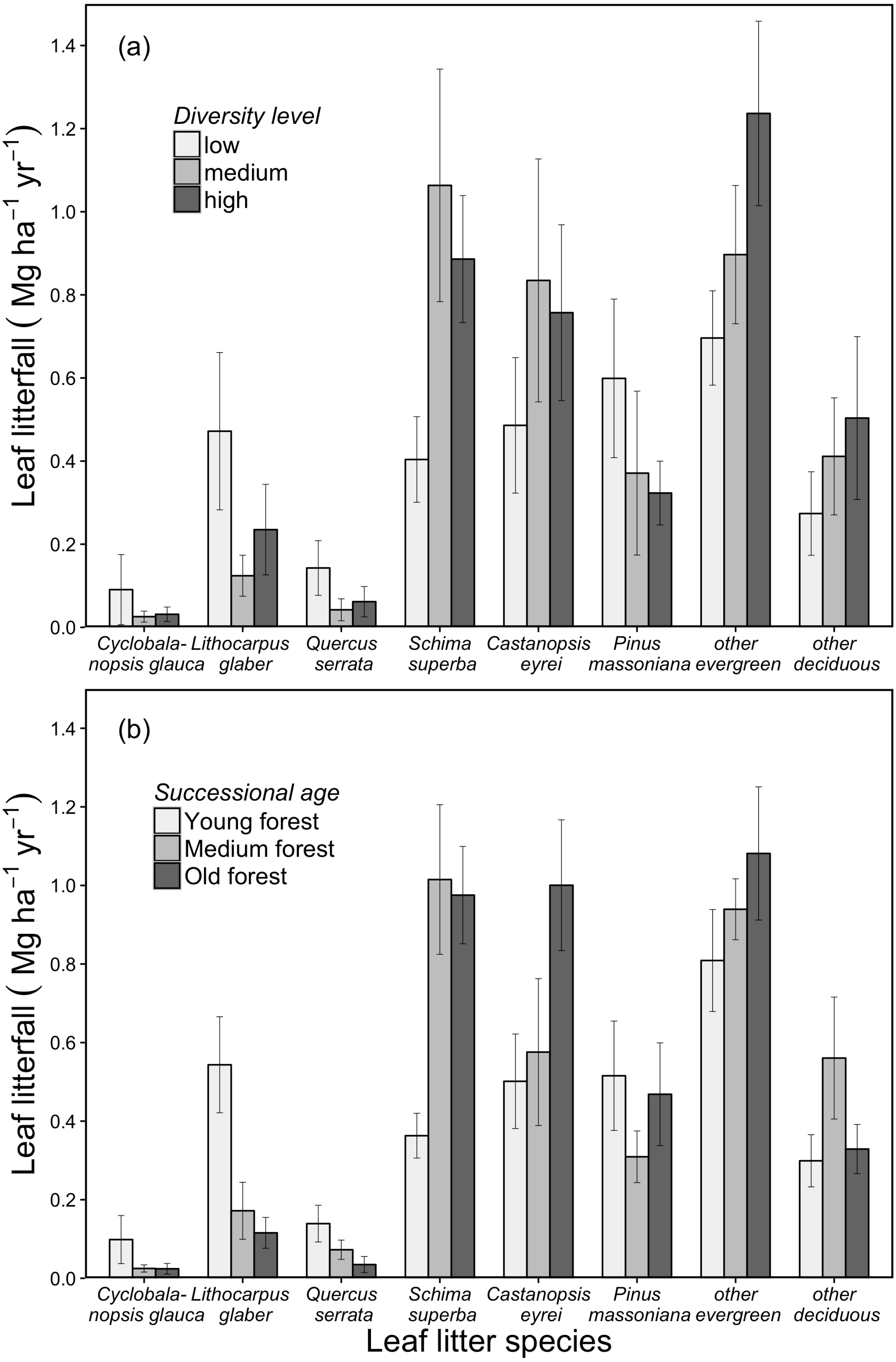
(a)
Diversity level
low
medium
high
Leaf litterfall (Mg ha−1 yr−1)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Cyclobala-nopsis glauca
Lithocarpus glaber
Quercus serrata
Schima superba
Castanopsis eyrei
Pinus massoniana
other evergreen
other deciduous
(b)
Successional age
Young forest
Medium forest
Old forest
Leaf litterfall (Mg ha−1 yr−1)
Leaf litter species

Figure 6: production of different species' leaf litter at (a) different species richness levels and (b) along different successional stages (see legends inside figure). Error bars indicate means ± standard errors (n = 9).